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Accessibility

Forest ecosystem changes from annual methane source to sink depending on late summer water balance

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Key Points

Summer precipitation may moderate a methane source-sink transition at this site

Ecosystem-scale photosynthesis correlates with methane fluxes over short and long timescales

Multiyear flux datasets are needed to build predictive understanding

Abstract

Forests dominate the global carbon cycle, but their role in methane (CH_4) biogeochemistry remains uncertain. We analyzed whole-ecosystem CH_4 fluxes from two years, obtained over a lowland evergreen forest in Maine, USA. Gross primary productivity (GPP) provided the strongest correlation with the CH_4 flux in both years, with an additional significant effect of soil moisture in the second, drier, year. This forest was a neutral to net source of CH_4 in 2011 and a small net sink in 2012. Inter-annual variability in the summer hydrologic cycle apparently shifts the ecosystem from being a net source to a sink for CH_4. The small magnitude of the CH_4 fluxes and observed control or CH_4 fluxes by forest productivity and summer precipitation provide novel insight into the CH_4 cycle in this globally important forest ecosystem.

Introduction

Global forests remove CO_2 from the atmosphere at a rate of ~2.4 Pg C per year [*Pan et al.*, 2011]. The role of forests in methane (CH_4) cycling, however, has not been well constrained, in part because of difficulties in assessing CH_4 fluxes at the landscape scale. Most of what is known about forest CH_4 fluxes is derived from chamber measurements at the level of the soil surface, which show that many forest soils are net consumers of atmospheric CH_4 [*Megonigal and Guenther*, 2008]. Globally, CH_4-consuming bacteria in terrestrial soils are believed to account for approximately 5% of total CH_4 oxidation, the second largest sink of atmospheric CH_4 while anaerobic (saturated) soils are strong sources of CH_4 [*Forster et al.*, 2007]. The division between what constitutes a CH_4 producing vs consuming soil is murky with upland soils demonstrated to emit CH_4 under

41 certain circumstances [*Savage et al.*, 1997; *Whalen et al.*, 1991; *Yavitt et al.*, 1995; *Yavitt*
42 *et al.*, 1990] and localized (often discrete) soil flux measurements are difficult to scale up
43 due to their high spatial and temporal variability.

44 Forests with high water tables and organic-rich soils, such as many boreal forests,
45 provide an especially complex picture with dry and wet soil conditions intermixed due to
46 small-scale topographic variability. Such forests have the most potential to produce and
47 emit significant quantities of CH_4. In addition, direct interaction of trees with forest CH_4
48 emissions have also been posited, either aerobically [*Keppler et al.*, 2006], through
49 internal anaerobic rot [*Covey et al.*, 2012], or with the trees acting as conduits for soil-
50 produced CH_4 dissolved in the transpiration stream [*Nisbet et al.*, 2009; *Pangala et al.*,
51 2013]. Determining what controls the magnitude and seasonality of forest CH_4 fluxes
52 above the canopy will define the roles of forest soils and trees in the global CH_4 cycle.

53 Recent improvements in fast-response CH_4 analyzers have made it possible to measure
54 ecosystem-scale CH_4 fluxes by eddy covariance [*Peltola*, 2011; *Smeets et al.*, 2009;
55 *Wang et al.*, 2013]. Here we present and analyze the first multi-year eddy covariance time
56 series of CH_4 fluxes from a forested ecosystem. The results show that the site was a
57 neutral to small net source of CH_4 during 2011 but a net sink during 2012. Importantly,
58 no strong CH_4 sources, either from the soils or trees, are indicated by this study. The
59 strongest correlate for the 4-day averaged CH_4 flux dynamics was GPP during both years,
60 with soil moisture accounting for significant variance during dry periods. Our results
61 suggest that multi-year studies will be critical to developing model structures capable of
62 reproducing net fluxes and predicting changes in future CH_4 fluxes from forested
63 ecosystems.

Methods

Site Description

Research was conducted at the Howland Forest AmeriFlux site located about 35 miles north of Bangor, Maine, USA (45°15' N, 68°44' W, 60 m asl) on forestland owned by the Northeast Wilderness Trust. Howland Forest is a boreal-temperate transition forest, with stands dominated by red spruce (*Picea rubens* Sarg.) and eastern hemlock (*Tsuga canadensis* (L.) Carr.) with lesser quantities of other conifers and hardwoods. The soils have never been cultivated and the upland soils are classified as Skerry fine sandy loam, Aquic Haplorthods. Peats have formed in the poorly drained positions dominated by sphagnum. Fernandez et al. [1993], and Hollinger et al. [1999; 2004] have previously described the climate, soils, and vegetation at the site.

Flux measurements

Fluxes were measured at a height of 29 m with systems consisting of a model SAT-211/3K 3-axis sonic anemometer (Applied Technologies Inc., Longmont, CO, USA) and a fast-response $CH_4/CO_2/H_2O$ cavity ring down spectrometer (model G1301-f in 2011 and G2311-f in 2012; Picarro Inc., Santa Clara, CA) with data recorded at 5 Hz. The CO_2 flux measurements were also independently quantified with a co-deployed fast response CO_2/H_2O infrared gas analyzer (model Li-7200, Li-Cor Inc., Lincoln, NE, USA). In 2011, H_2O concentrations measured with the Li-7200 were used for density correction of CO_2 and CH_4 fluxes measured with the G1301-f because that instrument could not output all three concentrations simultaneously. Fluxes were calculated and filtered according to Hollinger et al. [1999; 2004]. In 2012, fluxes were calculated via the same equations and assumptions (600 s time constant running mean filter, double rotation, etc.) using

87 commercially available software (EddyPro version 4, Li-Cor Inc., Lincoln, NE, USA). In
88 both years, the CO_2 fluxes were nearly identical between the Picarro and Licor analyzers
89 (Fig S1). The sign convention used is that flux to the ecosystem is defined as negative.
90 Further details on the filtering of the flux data are available in the SI.

91 *Environmental Data*

92 Profiles of soil temperature and soil moisture were measured hourly at 5, 10, 20, 50, and
93 100 cm using Hydra probes (Stevens Water Monitoring Systems Inc., Beaverton, OR,
94 USA) 20 near the base of the tower. Water table depth was measured using a
95 barometrically compensated pressure transducer (model WL400, Global Water, Gold
96 River, CA, USA) in a shallow well. Solar radiation (photosynthetic photon flux density,
97 PPFD), air temperature, and precipitation were measured from the top of the flux tower
98 as described previously [*Hollinger et al.*, 2004]. We note that the measurement scale for
99 the soil data differs from that of the flux data.

100 *Statistical Analyses*

101 The half-hourly CH_4 flux data were low-pass filtered to give a set of mean fluxes, each
102 representing a 4-day window. This was combined with Monte-Carlo resampling in order
103 to obtain an estimate of the uncertainty on these mean fluxes. Details are available in the
104 SI.

105 We used an Artificial Neural Network (ANN) to characterize the climatic sensitivity of
106 ecosystem-atmosphere CH_4 exchange and to estimate annual CH_4 budgets. This
107 methodology choice is supported by a recent study showing the effectiveness of ANNs
108 for gap-filling CH_4 fluxes [*Dengel et al.*, 2013]. An ANN is an inductive approach based

on statistical multivariate modeling [*Bishop*, 1995; *Rojas*, 1996] by which one can map drivers directly onto observations [*Moffat et al.*, 2010]. We used a feed-forward ANN with a sigmoid activation function trained with a back propagation algorithm. An ensemble of 100 ANNs was trained both on the hourly and running mean aggregated eddy-covariance CH_4 fluxes independently. See SI for description of our 3-stage training process.

Results

Many variables including GPP, air temperature, PPFD, CO_2 flux, and soil moisture and soil temperature at 10 and 20 cm were significantly correlated (Kendall rank correlation, $p<<0.01$) with the CH_4 flux signal in both years, but any combination of these variables explains only a small fraction of the variation in the CH_4 fluxes (multiple $r^2<0.05$) at the 30 minute time step. The neural network approach was able to explain a maximum of 8-10% of the total variability in the data for each year (Fig S3) using a combination of environmental drivers (GPP, air temperature, wind direction, wind speed, relative humidity, soil moisture, soil temperature, and water table depth). The individual driver with the highest explanatory power in the ANN was air temperature in 2011 and GPP in 2012. These low correlations emerge because of the large random errors (noise) in the measurement, which argues for the use of statistical approaches for time averaging of the data to reduce uncertainties and permit elucidation of the trends.

Averaging the fluxes by time of day, we observed more CH_4 efflux during the daytime and more CH_4 consumption at night. This pattern was only present during summer months (Fig S4). We used a wavelet coherence analysis as an alternate approach for examining the significance of this diurnal structure. Using this analysis we found

132 coherent periodic behavior in both the CH_4 and GPP signals at the 18-28 hour time scale
133 over the summer and early fall seasons, although the time periods when this relationship
134 was significant were intermittent. The coherence between the CH_4 flux and GPP signals
135 was stronger than between CH_4 flux and air temperature. Due in part to the intermittent
136 nature of the coherence, it was not possible to determine whether CH_4 flux lagged GPP,
137 which could potentially indicate a causal relationship.

138 The use of 4-day mean fluxes elucidated the seasonal pattern in the CH_4 flux data. CH_4
139 fluxes were mostly positive during the summer months, trending negative in the late
140 summer or fall, then remaining consistently negative through the winter months (Fig 1).
141 By comparison, the CO_2 fluxes (here processed as GPP) showed the opposite pattern with
142 the highest rates of CO_2 uptake during the midsummer, followed by decreasing uptake
143 through the fall into the winter.

144 The spring and summer precipitation patterns differed between 2011 and 2012. While the
145 total annual precipitation measured at the tower was lower in 2011 (870 mm) than in
146 2012 (940 mm), the precipitation during July and August was much greater during 2011
147 than 2012 (224 vs 76 mm). This precipitation change led to a large difference in
148 summer/fall soil moisture between the years (Fig 1). Historical precipitation data
149 (http://www.ncdc.noaa.gov/cdo-web/) from Millinocket station (located ~50 km north of
150 Howland forest) for July and August for 1970-2010 gives a mean (± 1sd) precipitation of
151 200 ± 73 mm for those months combined. In 2011 Millinocket recorded July-August
152 precipitation of 282 mm during 2011, compared with 127 mm for 2012, indicating that
153 2011 was wetter than the 40-yr average whereas 2012 was drier than average.

154 Using a wide selection of variables (air temperature, soil temperature, soil moisture, wind
155 direction, water table depth, relative humidity, and wind speed) the ANN produced a
156 model explaining nearly 65% and 90% of the variability in the 4-day CH_4 fluxes during
157 2011 and 2012. However, to reduce the redundancy due to correlations between many of
158 these drivers, we forced the ANN to use GPP and then tested for the additional
159 explanatory power (if any) attained by each remaining driver (Fig 2, S5). GPP was
160 chosen because it was the individual variable with the highest explanatory power in both
161 years. The importance of each driver using this reduced approach is shown in Fig 2. We
162 observe that, in 2011 and 2012 respectively, variation in GPP accounted for 60% and
163 50% of the variability in the 4-day CH_4 fluxes. Including soil moisture increases the
164 explanatory power of the model by >10% during 2012 (the drier year) but has negligible
165 influence in 2011 (the wetter year). Therefore, a model using only GPP and 10-cm soil
166 moisture was able to explain ~ 60 and 70% of the variability in 4-d mean CH_4 fluxes for
167 2011 and 2012. All other drivers provide negligible improvement to the model fit. This
168 order of importance of drivers was supported by separate linear regression analysis
169 (Table S1).

170 Despite the fact that the principal environmental drivers were the same in both years,
171 models derived from the 2011 fluxes did a poor job predicting CH_4 fluxes in 2012, and
172 vice versa (Fig. S6). We also trained the model on the 4-day means from both years
173 together and while the ANN produced a model that explained 40% of the variability in all
174 the data this represented a substantial decrease in goodness-of-fit compared to modeling
175 each year individually.

We estimated the annual CH_4 budgets for 2011 and 2012 for Howland forest in two ways; using either the ANN or a linear model combined with Monte Carlo resampling. Using the linear modeling approach (Fig S7) we estimate net efflux (mean ± 1sd) of 7 ± 4.6 mmol m^{-2} yr^{-1} for 2011 and consumption -18 ± 2.7 mmol m^{-2} yr^{-1} for 2012. Using the ANN, annual fluxes were 6 ±11 mmol m^{-2} yr^{-1} for 2011, and -9 ± 3.7 mmol m^{-2} yr^{-1} for 2012 (Fig 2). Larger uncertainties were contributed by the first few months of the year due to the absence of measurements to constrain the model during these periods. This increase in variance was particularly large in the ANN because of its inherently nonlinear structure. Both approaches indicated that the annual CH_4 flux in 2011 was small but likely positive while the forest was a net consumer of CH_4 in 2012.

Discussion

The lowland evergreen forest studied was an intermittent source of CH_4 to the atmosphere, showing efflux from July through October during 2011, and from June through July 2012 while recording net uptake for the remainder of each year (Fig 1). Using an artificial neural network (ANN), we found that a combination of GPP and 10-cm soil moisture was able to explain 60 and 70% of the variability in 4-d mean CH_4 emissions for 2011 and 2012 individually (Fig 2), while use of all the drivers resulted in a model explaining nearly 90% of the variability during 2012 (the maximum explainable variance in 2011 is just above 60%). Additionally, a diurnal cycle was present in the CH_4 flux signal during the summer and fall that was consistent with that observed in GPP. The ANN, supported by linear modeling, consistently found GPP to be a stronger correlate of the 4-day mean CH_4 fluxes than air temperature.

198 Gross primary production is highly correlated with a wide variety of other environmental
199 parameters, such as air temperature, PPFD, and soil temperature, and it could be argued
200 that GPP is driving CH_4 emissions only indirectly through cross-correlations. The a priori
201 assumption would be that CH_4 fluxes are controlled by soil moisture [*Adamsen and King*,
202 1993; *Castro et al.*, 1994; *Castro et al.*, 1995] due to the dependence of both CH_4
203 oxidation and CH_4 production on soil diffusivity (through O_2 availability) with
204 temperature being a secondary controlling variable [*Castro et al.*, 1995] due to the
205 positive influence of temperatures on reaction rates (positive Q10 values). However, both
206 the neural network and linear modeling approaches found GPP to be the stronger
207 predictor of CH_4 emissions when treating each year individually, or together, with soil
208 moisture only important during 2012.

209 There are several mechanistic reasons why changes in GPP may lead to changes in CH_4
210 emissions. First, CH_4 production rates have been linked to photosynthesis through root
211 exudation in some wetlands [*King and Reeburgh*, 2002]. Carbon isotope studies have
212 shown that most CH_4 released from wetlands is derived from “new carbon” rather than
213 from dissolved soil organic matter [*Chanton et al.*, 1995] . In a rice paddy, wavelet
214 coherence analysis found the diurnal cycle in CH_4 emissions to be driven by GPP [*Hatala*
215 *et al.*, 2012]. However, trees may also be influencing the seasonal and diurnal cycle if
216 dissolved CH_4 is emitted through transpired soil water [*Nisbet et al.*, 2009], such that
217 GPP could be more proxy than mechanism. It is more difficult to directly connect CH_4
218 oxidation and GPP, although microbial priming could link these processes. In this case,
219 carbon leakage from the roots of trees and other plants increases total microbial activity;
220 because many CH_4 oxidizing bacteria are capable of consuming a wide variety of

221 methylated substrates their population dynamics could respond to overall soil carbon
222 degradation rates, leading to higher rates of CH_4 oxidation linked to increased soil
223 respiration activity. We interpret these results as indicating a significant role for GPP in
224 influencing CH_4 flux, both in its high frequency and low frequency variability although
225 we acknowledge that the mechanism is not yet clear.

226 The role of soil moisture in forest CH_4 flux may involve a threshold: once volumetric soil
227 moisture exceeds some level (here ~0.1WFV), there are sufficient anoxic pore spaces to
228 support CH_4 production near the surface and correlations become weak, while below this
229 threshold, soil moisture is an important factor controlling the balance between CH_4
230 production and CH_4 oxidation. It is also possible that the lower correlations are a result of
231 spatial variability in soil moisture over the tower footprint related to the small-scale
232 topography that was not captured by this study. However, the trends of drying and
233 wetting, also observed in the precipitation data, would be expected to be felt to some
234 degree throughout the landscape. Overall, we found soil moisture had a smaller overall
235 influence than GPP but remains important under drier conditions.

236 Despite the high correlations of a model using GPP and soil moisture to the data in each
237 year, the explanatory power of these models diminished almost to zero when applied to
238 data on which the model was not trained (Fig S6). Similar challenges have been observed
239 with modeling CH_4 fluxes [*Mastepanov et al.*, 2012; *Moore et al.*, 2011; *Treat et al.*,
240 2007], as well as CO_2 fluxes [*Richardson et al.*, 2007] from a variety of environments.
241 Net CH_4 emission is the result of two processes acting in opposition – CH_4 production
242 and CH_4 oxidation, and it appears that a correlative model based on emissions may lack
243 the appropriate structure needed to extrapolate fluxes over longer timescales, despite

244 success over shorter timescales. Achieving an appropriate model structure and
245 complexity is necessary for improving the CH_4 components of larger earth-system
246 models and predicting natural CH_4 emissions from forests under changing environmental
247 conditions. Multiple years of flux measurements under a range of conditions will be
248 needed to accurately characterize the climatic and physiological dependence of forest
249 CH_4 fluxes. Experimental methods combining ecosystem-scale flux measurements, soil
250 chamber flux measurements, and soil-gas profiles may also provide needed insight into
251 the mechanistic controls driving both the sign and magnitude of CH_4 flux.

252 In the context of the overall climate impact of greenhouse gas fluxes at this site, the CH_4
253 fluxes are small contributors (see SI) relative to the total CO_2 uptake. This contrasts with
254 other ecosystems, such as boreal wetlands where the climate impact of CH_4 fluxes can be
255 larger than the climate benefit of their CO_2 uptake [*Whiting and Chanton*, 2001].

256 **Conclusions**

257 We provide the first multi-year set of CH_4 fluxes measured by eddy-covariance over a
258 forested ecosystem. Multi-year data sets of CH_4 fluxes capturing a wide variety of
259 environmental conditions are critical to developing model structures that are capable of
260 adequately predicting future CH_4 fluxes. GPP provided the strongest correlation with the
261 calculated 4-day mean CH_4 fluxes during each year. Including soil moisture as a driver
262 for CH_4 production improved the fit of the model only during 2012, which had a drier
263 than average summer. Despite the potential for CH_4 efflux from this temporate-boreal
264 transition site, our observations suggest that neither the soils nor trees are large sources of
265 CH_4 from the forest to the atmosphere. This study finds evidence for a link between GPP

and CH_4 flux, and a small sink/source transition controlled by summer hydrologic conditions.

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364 **Figure Legends**

365 Figure 1: The 4-day running mean CH_4 fluxes (open circles) with 4-day mean GPP (grey
366 stars) and volumetric soil moisture at 10 cm (black squares). Data from 2011 is shown in
367 the top panel against data from 2012 in the lower panel. The dotted black line highlights
368 the line of 0 flux, above which the forest is a net source of CH_4 to the atmosphere and
369 below which the forest is a net sink for CH_4.

370 Figure 2: Results from the ANN for both years, with the top panels indicating the
371 importance of various environmental drivers contributing to the model. Each
372 environmental driver is shown separately with the black portion of the column indicating
373 the additional predictive power this driver gives the model when combined with GPP (the
374 grey portion of the column). The horizontal dotted lines indicate the maximum attainable
375 predictive capacity if all drivers are used simultaneously. The bottom panels show the
376 ANN modeled fluxes for the entire year (black lines) ± 1 sd (vertical bars).